


ORIGINAL ARTICLE OPEN ACCESS

Multiple Trait Bayesian Analysis of Partitioned Genetic Trends Accounting for Uncertainty in Genetic Parameters. An Example With the Pirenaica and Rubia Gallega Beef Cattle Breeds

David López-Carbonell¹  | Andrés Legarra²  | Juan Altarriba¹  | Carlos Hervás-Rivero¹  | Manuel Sánchez-Díaz¹  | Luis Varona¹ 

¹Genética Cuantitativa y Mejora Animal, Universidad de Zaragoza, Instituto Agroalimentario de Aragón (IA2), Zaragoza, Spain | ²CDCB, Bowie, Maryland, USA

Correspondence: David López-Carbonell (davidlc@unizar.es)

Received: 24 July 2024 | **Revised:** 18 November 2024 | **Accepted:** 30 November 2024

Funding: This study was financed by the project PASTORCLIM (Ref. EFA 077/01). It was supported by the European Regional Development Fund (Fondo Europeo de Desarrollo Regional, FEDER) at 65% through the Interreg VI-A Spain-France-Andorra Program (POCTEFA 2021–2027). The objective of POCTEFA is to strengthen the economic and social integration of the Spain-France-Andorra border area. David López Carbonell received funding from the Strategic Grant Plan of the Department of Science, University, and Knowledge Society 2020–2023 of the Government of Aragon.

ABSTRACT

Genetic trends are a valuable tool for analysing the efficiency of breeding programs. They are calculated by averaging the predicted breeding values for all individuals born within a specific time period. Moreover, partitioned genetic trends allow dissecting the contributions of several selection paths to overall genetic progress. These trends are based on the linear relationship between breeding values and the Mendelian sampling terms of ancestors, enabling genetic trends to be split into contributions from different categories of individuals. However, (1) the use of predicted breeding values in calculating partitioned genetic trends depends on the variance components used and (2) a multiple trait analysis allows accounting for selection on correlated traits. These points are often not considered. To overcome these limitations, we present a software called “TM_TRENDS.” This software performs a Bayesian analysis of partitioned genetic trends in a multiple trait model, accounting for uncertainty in the variance components. To illustrate the capabilities of this tool, we analysed the partitioned genetic trends for five traits (Birth Weight, Weight at 210 days, Cold Carcass Weight, Carcass Conformation, and Fatness Conformation) in two Spanish beef cattle breeds, Pirenaica and Rubia Gallega. The global genetic trends showed an increase in Carcass Conformation and a decrease in Birth Weight, Weight at 210 days, Cold Carcass Weight, and Fatness Conformation. These trends were partitioned into six categories: non-reproductive individuals, dams of females and non-reproductive individuals, dams of sires, sires with fewer than 20 progeny, sires between 20 and 50 progeny, and sires with more than 50 progeny. The results showed that the main source of genetic progress comes from sires with more than 50 progenies, followed by dams of males. Additionally, two additional features of the Bayesian analysis are presented: the calculation of the posterior probability of the global and partitioned genetic response between two time points, and the calculation of the posterior probability of positive (or negative) genetic progress.

This is an open access article under the terms of the [Creative Commons Attribution-NonCommercial](https://creativecommons.org/licenses/by-nc/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited and is not used for commercial purposes.

© 2024 The Author(s). *Journal of Animal Breeding and Genetics* published by John Wiley & Sons Ltd.

1 | Introduction

The assessment of the efficiency of selection breeding program has traditionally relied on calculating genetic trends (Blair and Pollak 1984; Sorensen and Kennedy 1984). These trends are determined by averaging the predicted breeding values for all individuals born within a specific time period. Breeding values are predicted using best linear unbiased prediction (BLUP) through mixed model equations (Henderson 1984). However, this approach yields a global genetic trend without offering insights into the efficiency of breeding decisions for specific groups of individuals. To address this limitation, partitioned genetic trends were introduced (García-Cortés, Martínez-Ávila, and Toro 2008). This approach divides the breeding values into several components, each attributed to the Mendelian sampling terms or the founder effects of a specific group of individuals (e.g., sires vs. dams).

Recently, this method has been implemented in an R (R Core Team. 2021) package called AlphaPart (Obšteter et al. 2021). AlphaPart has been utilised in evaluating genetic trends in dairy sheep (Antonios et al. 2023), pigs (Abdollahi-Arpanahi et al. 2021), and cattle (Obšteter et al. 2023). AlphaPart software can be used with predicted breeding values from genetic evaluations generated by other software tools, such as DMU (Madsen et al. 2010) or BLUPF90 (Misztal et al. 2018). However, it does not account for the uncertainty associated with heritability or variance components. This uncertainty can be addressed by applying partitioned genetic trends within a Bayesian approach (Sorensen et al. 1994), as implemented by Škorput et al. (2015) in Croatian Landrace and Large-White pigs. Moreover, a recent study employs a full Bayesian approach with simulated data to partition genetic mean and variance (Oliveira et al. 2023). However, this method requires the use of AlphaPart software with the breeding value samples from each iteration of the Gibbs sampler.

In livestock breeding programs, some traits may only be recorded in a small subset of individuals, and phenotypic information from correlated traits can provide valuable insights into predicting breeding values (Thompson and Meyer 1986). In particular, using multiple trait analysis allows studying genetic change due to selection on correlated traits, for example, yield and fertility, or growth and carcass traits. Not using this information leads to “non-ignorable” selection, leading to wrong results (Im, Fernando, and Gianola 1989; Sorensen and Kennedy 1984). As an example, it is the case of carcass quality traits, which are not recorded in selected individuals. Some studies have used multiple trait analysis to partition genetic trends (Abdollahi-Arpanahi et al. 2021; Škorput et al. 2015). However, these genetic trends were computed from BLUP solutions or posterior mean estimates of breeding values, without calculating their confidence or highest posterior density intervals. Therefore, the objective of this study is to present a new software (TM_TRENDS—https://github.com/david20011999/TM_TRENDS.git) based on the TM software (Legarra, Varona, and López de Maturana 2011), that allows for the calculation of a multiple-trait Bayesian analysis of partitioned genetic trends. This new software simultaneously performs Bayesian estimation of posterior distributions for variance components, breeding values, and partitioned genetic trends, all within a single execution.

Unlike the approach described by Oliveira et al. (2023), it eliminates the need for additional post-processing of each Markov Chain Monte Carlo samples. To illustrate its application, we developed an example investigating the genetic response and its uncertainty for five traits (Birth Weight [BW], Weight at 210 days [W210], Cold Carcass Weight [CCW], Carcass Conformation [CONF], and Carcass Fatness [FAT]) in two Spanish beef cattle breeds: Pirenaica and Rubia Gallega.

2 | Materials and Methods

The phenotypic and genealogical datasets used in the study were collected by CONASPI (Confederación Nacional de Asociaciones de Criadores de Ganado Pirenaico) for Pirenaica and ACRUGA (Asociación Nacional de Criadores de Ganado Vacuno Selecto de Raza Rubia Gallega) for Rubia Gallega. Traits BW and W210 were recorded on farm, with weight records between 170 and 250 days of age assigned to W210. Traits CCW, CONF, and FAT were recorded at the slaughterhouse. The average age at slaughter was 373.63 days (with a standard deviation of 41.76 days) for Pirenaica and 275.27 days (with a standard deviation of 25.80 days) for Rubia Gallega populations, respectively. CONF was described using the SEUROP scale and converted into a numeric scale from 1 (P–, worst) to 18 (S+, best). FAT was scaled from 1 (low) to 15 (high), as described in Altarriba et al. (2009). Table 1 presents the number of records, as well as the phenotypic means and standard deviations for each trait.

The Pirenaica pedigree included 306,547 individual-sire-dam entries, while the Rubia Gallega population had 429,068 entries. All individuals registered from 1992 were included in the pedigree. Parents of these individuals born before 1992 were included and settled the founder population. Before 1990, data recording was not a well-established process, thence missing or wrong records are frequent. With this process, spurious associations and uncertainty can be reduced in the founder population associated with data recording process problems.

TABLE 1 | Mean ± standard deviation and number of records (between brackets) for Birth Weight, Weight at 210 days, Cold Carcass Weight, Carcass Conformation, and Carcass Fatness in the Pirenaica and Rubia Gallega populations.

Trait		Breed	
		Pirenaica	Rubia Gallega
Birth Weight		41.17 ± 4.46 (158,955)	42.72 ± 7.07 (354,955)
	Weight at 210 days	254.00 ± 58.32 (41,938)	285.74 ± 47.79 (101,414)
Cold Carcass Weight		300.00 ± 56.21 (107,887)	224.18 ± 41.13 (100,683)
	Carcass Conformation	11.88 ± 1.35 (103,180)	10.91 ± 1.99 (100,619)
Carcass Fatness		6.32 ± 1.20 (99,056)	5.78 ± 1.32 (100,536)

Data were analysed with the following statistical model:

$$\mathbf{y}_t = \mathbf{X}_t \mathbf{b}_t + \mathbf{W}_t \mathbf{p}_t + \mathbf{Z}_t \mathbf{u}_t + \mathbf{e}_t$$

where \mathbf{y}_t is the vector of phenotypes for the t ($t = \{\text{BW}, \text{W210}, \text{CCW}, \text{CONF}, \text{FAT}\}$ trait); \mathbf{b}_t is the vector of systematic effects (sex and age of dam for BW; a covariate with the age plus sex and age of dam for W210, and a covariate with the age plus sex and slaughterhouse for CCW, CONF and FAT); \mathbf{p}_t is the vector of random herd-year-season effects; \mathbf{u}_t is the vector of the additive genetic effects; and \mathbf{e}_t is the vector of residuals. Furthermore, \mathbf{X}_t , \mathbf{W}_t , and \mathbf{Z}_t are the respective incidence matrices that links the systematic, herd-year-season, and additive genetic effects with the phenotypic records.

The vector of the additive genetic effects and the residuals are assumed to be multivariate Gaussian:

$$\begin{pmatrix} \mathbf{u}_{\text{BW}} \\ \mathbf{u}_{\text{W210}} \\ \mathbf{u}_{\text{CCW}} \\ \mathbf{u}_{\text{CONF}} \\ \mathbf{u}_{\text{FAT}} \end{pmatrix} \sim N(\mathbf{0}, \mathbf{A} \otimes \mathbf{G}), \quad \begin{pmatrix} \mathbf{e}_{\text{BW}} \\ \mathbf{e}_{\text{W210}} \\ \mathbf{e}_{\text{CCW}} \\ \mathbf{e}_{\text{CONF}} \\ \mathbf{e}_{\text{FAT}} \end{pmatrix} \sim N(\mathbf{0}, \mathbf{I} \otimes \mathbf{R})$$

where \mathbf{G} and \mathbf{R} are the additive and the residual (co)variances matrices, respectively. Furthermore, \mathbf{A} is the numerator additive relationship matrix. The herd-year-season effects for BW and W210 were assumed to be $N(0, \sigma_{p(\text{BW})}^2)$ and $N(0, \sigma_{p(\text{W210})}^2)$, where $\sigma_{p(\text{BW})}^2$ and $\sigma_{p(\text{W210})}^2$ are the herd-year-season variances associated with the herd of birth and herd of recoding W210. Finally, the herd-year-season effects for CCW, CONF, and FAT follow a multivariate Gaussian distribution:

$$\begin{pmatrix} \mathbf{p}_{\text{CCW}} \\ \mathbf{p}_{\text{CON}} \\ \mathbf{p}_{\text{FAT}} \end{pmatrix} \sim N(\mathbf{0}, \mathbf{I} \otimes \mathbf{M})$$

where \mathbf{M} is the herd-year-season (co)variance matrix associated with the herd of growth. Prior distributions for the variance components and the systematic effects were assumed uniform.

The implementation of the Gibbs sampler is equivalent to that used in the original TM software (Legarra, Varona, and López de Maturana 2011). Specifically, the multi-trait implementation of the Gibbs sampler is based on Van Tassell and Van Vleck (1996), that involves sampling from the conditional distributions of each level of the systematic, random, and additive genetic effects, which follow univariate Gaussian distributions, as well as from the conditional distributions of the variance components, which follow inverted Wishart distributions.

To develop the partitioning of genetic trends, the vector of breeding values for each trait (\mathbf{u}_t) was described as a linear combination of the Mendelian sampling terms ($\boldsymbol{\phi}$) and the breeding values of the founders, following the approach suggested by García-Cortés, Martínez-Ávila, and Toro (2008). Thus, $\mathbf{u}_t = \mathbf{T}\boldsymbol{\phi}_t$, where \mathbf{T} is a triangular matrix that models

the flow of the genes through the pedigree (Woolliams, Bijma, and Villanueva 1999). Furthermore, García-Cortés, Martínez-Ávila, and Toro (2008) proposed defining a set of partitions based on cluster or groups of individuals ($\mathbf{P}_1 + \mathbf{P}_2 + \mathbf{P}_3 + \dots + \mathbf{P}_k = \mathbf{I}$). The \mathbf{P}_i are diagonal matrices with ones in the diagonal if the individual belong to the i th cluster and zero otherwise. Then,

$$\mathbf{u}_t = \mathbf{T}(\mathbf{P}_1 + \mathbf{P}_2 + \mathbf{P}_3 + \dots + \mathbf{P}_k)\boldsymbol{\phi}_t$$

Replacing the Mendelian terms by $\boldsymbol{\phi}_t = \mathbf{T}^{-1}\mathbf{u}_t$:

$$\mathbf{u}_t = \mathbf{T}\mathbf{P}_1\mathbf{T}^{-1}\mathbf{u}_t + \mathbf{T}\mathbf{P}_2\mathbf{T}^{-1}\mathbf{u}_t + \mathbf{T}\mathbf{P}_3\mathbf{T}^{-1}\mathbf{u}_t + \dots + \mathbf{T}\mathbf{P}_k\mathbf{T}^{-1}\mathbf{u}_t$$

$$\mathbf{u}_t = \mathbf{u}_{t(1)} + \mathbf{u}_{t(2)} + \mathbf{u}_{t(3)} + \dots + \mathbf{u}_{t(k)}$$

where $\mathbf{u}_{t(k)} = \mathbf{T}\mathbf{P}_k\mathbf{T}^{-1}\mathbf{u}_t$ represents the vector of the k th partition of the breeding values. The TM_TRENDS software implements this partitioning at each iteration of the Gibbs sampler. It computes the average of the partial breeding values for each year to estimate the posterior mean and the posterior standard deviation of the partitioned genetic trends for each trait. Additionally, the software generates a text file containing samples of partitioned and global genetic trends, which can be used to compute the posterior distributions.

Breeding strategies in beef cattle populations, such as the Pirenaica and Rubia Gallega breeds, involve several selection decisions: (a) selection of dams, (b) identification of dams of future males, (c) selection of future sires, (d) selection of best young males by progeny testing, and (e) selection of the best males among the progeny tested to widespread the selection response all over the population. Therefore, the individuals of the pedigree were categorised into the following six clusters:

- Non-reproductive (NR): Individuals in the pedigree without any progeny.
- Dams of females and NR (DFNR): Dams of NR females and of individuals without progeny. Note that they are not dam of any sire.
- Dams of sires (DS).
- Sires with a progeny lower than 20 (S20).
- Sires with a progeny between 20 and 50 (S50).
- Sires with a progeny larger than 50 (S+).

Table 2 provides a summary of the distribution across these clusters.

In this work, for both breeds, the procedure involved a single chain of the Gibbs Sampler of 500,000 iterations, with the initial 100,000 iterations discarded for burn-in.

3 | Results and Discussion

The files needed for the implementation of the TM_TRENDS software are similar to those required for the original TM

TABLE 2 | Number of individuals allocated at each of the six clusters in the Pirenaica and Rubia Gallega populations.

Cluster	Breed	
	Pirenaica	Rubia Gallega
Non-reproductive	235,730	337,328
Dams of females and non-reproductive	62,422	87,746
Dam of sires	3528	1735
Sires with a progeny lower than 20	2009	956
Sires with a progeny between 20 and 50	1166	522
Sires with a progeny larger than 50	1692	761

(Legarra, Varona, and López de Maturana 2011) and are detailed in detail in the software documentation (see File S1). These files include a parameter file, a pedigree file and a data file. The parameter file contains the following information: (1) the names of the pedigree and data files; (2) the number of continuous and threshold traits; (3) the number of time units; (4) the number of clusters for partition the genetic trend; (5) the number of covariates, systematic and random effects, along with the number of levels for each effect; and (6) the initial values for the variance components, number of iterations, thinning interval and burn-in period for the Gibbs Sampler. The pedigree file provides individual identification, sire and dam information, along with unit time and cluster assignments. Finally, the data file includes covariates, systematic, and random effects, as well as the phenotypic records. An example of these files is provided in the software documentation (TM_TRENDS—https://github.com/david20011999/TM_TRENDS.git).

The TM_TRENDS software estimates variance components similarly to the original TM (Legarra, Varona, and López de Maturana 2011). Tables S1 and S2 present the posterior estimates of the heritabilities, genetic correlations, and residual correlations for the Pirenaica and Rubia Gallega, respectively. Furthermore, the posterior mean and standard deviation of the herd-year-season, additive and residual (co)variances are presented in Tables S3, S5, and S7 for Pirenaica and S4, S6, and S8 for Rubia Gallega.

The posterior mean estimates of the heritabilities, genetic and residual correlations align with previous findings in the same populations (Altarriba et al. 2009; López-Carbonell et al. 2023; Martínez-Castillero et al. 2021), as well as results observed in other populations (Hickey et al. 2007; Srivastava et al. 2019; Utrera and Van Vleck 2004). Comparing both breeds, Pirenaica exhibits higher heritability for BW and lower heritability for FAT compared to Rubia Gallega. The genetic correlations confirm previous research by Altarriba et al. (2009) in the Pirenaica population, showing positive correlations between BW and CCW, BW and CON, CCW and CONF and negative correlations between CONF and FAT. These correlations assist in predicting breeding values and estimating genetic trends. It is well known that using multiple trait models enhances the accuracy, especially for traits with low heritability traits and those with a strong correlation with another trait. Additionally, multi-trait models improve accuracy for individuals without phenotypic records. For instance, in the analysed dataset, many individuals

have recorded BW data, while only a subset has records for live (W210) or slaughterhouse-based (CCW, CONF, and FAT) traits. Thus, the phenotypic information for BW contributes to more accurate predictions of breeding values and genetic trends for W210, CCW, CONF, and FAT.

Figure 1 displays the posterior mean and highest posterior distribution with 95% probability (highest posterior densities [HPDs] 95) of the total genetic trends for BW, WW, CCW, CON, and FAT as estimated by the TM_TRENDS software. These results are obtained within the same software execution used for variance component estimation and breeding values prediction, eliminating the need of multiple runs of additional software to apply the partitioning method, as was done using AlphaPart software in Oliveira et al. (2023). This approach also addresses challenges related to memory costs and computational demands typically associated with R-based software if AlphaPart is used.

The genetic trend for BW showed a clear decline in the Pirenaica population, with the posterior standard deviation indicating that the genetic change is significantly different from zero. In contrast, the Rubia Gallega population exhibited a slight increase in BW until 1998, followed by a reduction and stabilisation since 2010. BW is a crucial trait in selection criteria aimed at reducing calving difficulties (Inoue, Hosono, and Tanimoto 2017). The difference of the genetic response between breeds can be associated with a higher selection pressure in Pirenaica.

W210 and CCW were positively genetically correlated (0.69 in Pirenaica and 0.48 in Rubia Gallega). Consequently, the genetic trends for both traits were very similar. Both populations showed a decrease in W210 and CCW until 2012. At this point, the Pirenaica population continued its reduction in both traits, while the Rubia Gallega reversed the genetic trends, showing an increase in W210 and CCW. In general, Spanish beef cattle breeds have been directed towards meeting market demands characterised by low carcass weights with high conformation (Piedrafita et al. 2003). The Rubia Gallega seems to follow a different trend, with larger animals slaughtered earlier. This trend is confirmed by the global genetic trends of FAT and CONF, which showed a positive trend in CONF and a negative trend in FAT. The SEUROP measure of CONF is directly linked to the price that farmers receive at slaughterhouses, making the improvement of CONF of high economic interest. The reduction in FAT may be attributed to the negative genetic correlation with CONF (−0.40 in Pirenaica and −0.63 in Rubia Gallega).

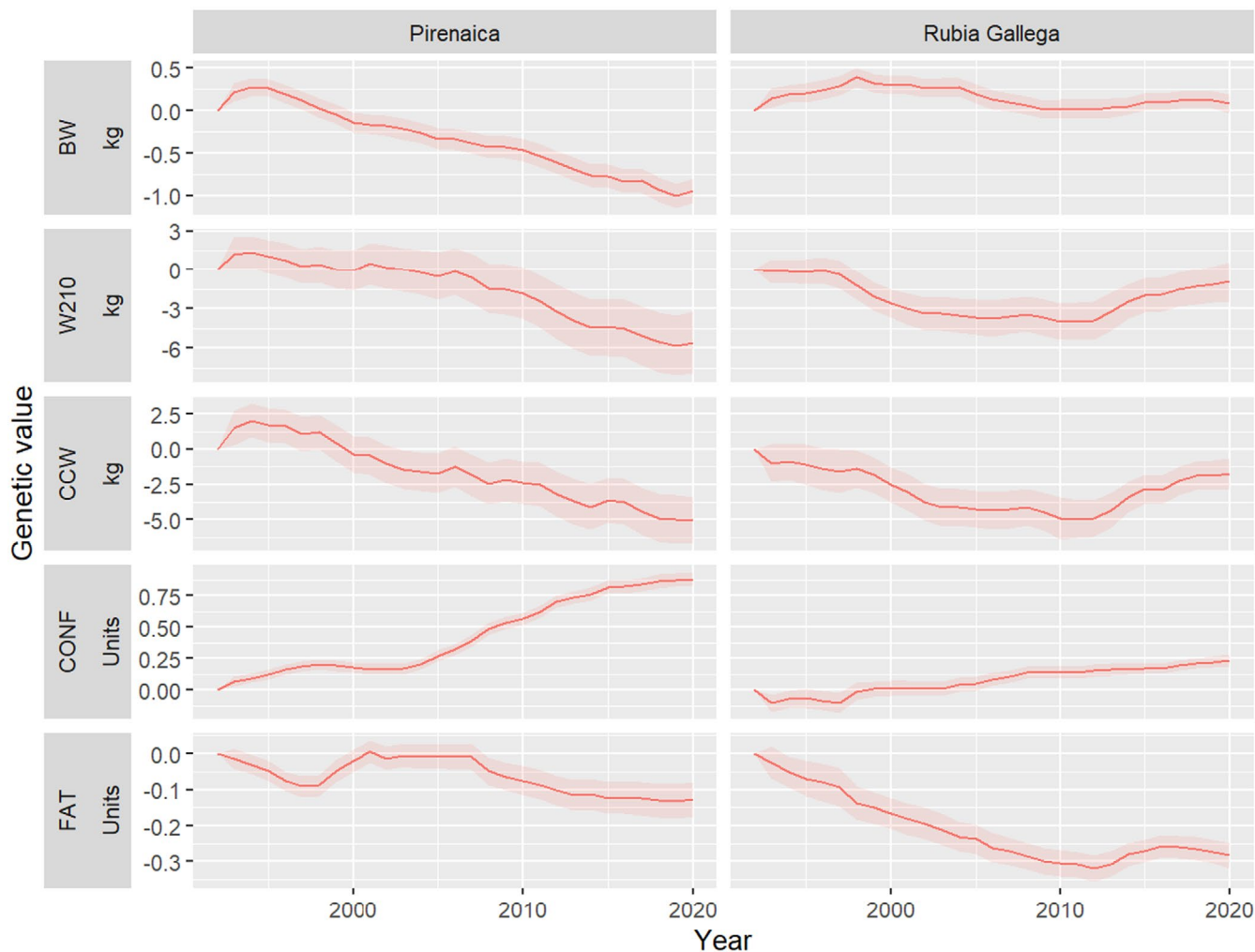


FIGURE 1 | Posterior mean (line) and highest posterior distribution with 95% probability (shadow) of the whole population genetic trends for Birth Weight (BW), Weight at 210 days (W210), Cold Carcass Weight (CCW), Carcass Conformation (CON), and Carcass Fatness (FAT) in Pirenaica (left) and Rubia Gallega (right) breeds. [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/jbr.12918)]

However, there are differences between the two populations: the slope of the genetic trend for CONF is steeper in Pirenaica than in Rubia Gallega, particularly after 2003 when SEUROP data were incorporated into the genetic evaluations of the breeding program. In contrast, the genetic trend for FAT in Rubia Gallega shows an inflection point around 2010, when the decline in FAT stopped and either stabilised or slightly increased. This can be associated with the slaughterhouse age of both breeds. The Rubia Gallega individuals are slaughtered younger than those from the Pirenaica to increase the tenderness of the meat. Because fat is deposited at late ages, the selection objective has changed so as not to decrease the quality of the meat.

The posterior means and HPD 95 of the partitioned genetic trends provided by the TM_TRENDS software are presented in Figure 2.

By analysing the posterior estimates of the partitioned genetic trends, it can be observed that most of the genetic response in both populations is primarily driven by the S+ sires. Indeed, the posterior distributions whose densities are clearly different from zero are those associated with these sires. The only exceptions to this are the genetic trends associated with DS, whose posterior

distributions are significantly different from zero in CONF for the Pirenaica population and in FAT for both populations. These results are similar to those described by Antonios et al. (2023) in dairy sheep, indicating that selection is linked to the choice of dams for future males and the final selection of AI sires. In contrast, almost no sign of selection is identified in natural service sires (those with fewer than 50 progeny), suggesting that selection efforts are focused on the preselection of dams for future sires. Moreover, the selection of dams does not provide any relevant genetic response, likely because the potential selection intensity for dams in beef cattle is very low.

It is important to note that in this case, a single group of founder individuals has been assigned in each breed, but TM_TRENDS also allows several founder groups to be assigned, and the genetic trends compared to them.

The TM_TRENDS software also outputs all Gibbs samples for the global and partitioned genetic trends. These values can be used to compute the posterior distribution for the genetic trends and any desired combination of them, which can be a valuable source of information to understand the effectiveness of a breeding program by groups. To illustrate this feature, Figure 3

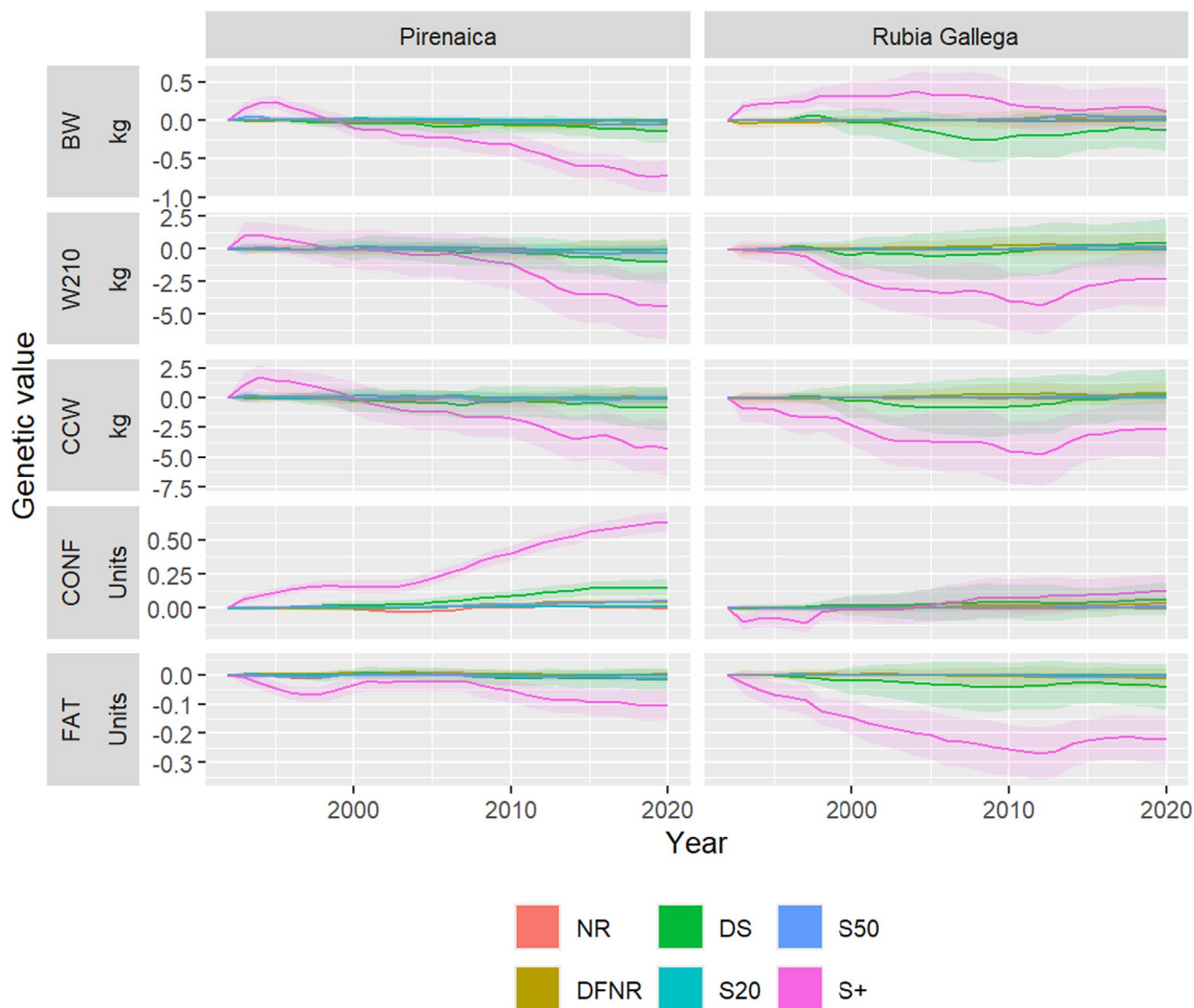


FIGURE 2 | Posterior mean (line) and highest posterior distribution with 95% probability (shadow) of the partitioned genetic trends in six different clusters (non-reproductive—NR-, Dams of dams and non-reproductive –DFNR-, Dam of Sires-DS-, Sires with a progeny lower than 20-S20-, Sires with a progeny between 20 and 49-S50-, and Sires with progeny higher than 50-S+-) for Birth Weight (BW), Weight at 210 days (W210), Cold Carcass Weight (CCW), Carcass Conformation (CONF), and Fatness (FAT) in Pirenaica (left) and Rubia Gallega breeds (right). [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

presents the posterior distributions of the global genetic difference in CONF for the two populations between individuals born in 1997 and 2007, and between 2007 and 2017, along with the genetic difference attributed to S+ and to the remain clusters of individuals during the same periods.

The figure shows that the total genetic progress in the Pirenaica population was more pronounced from 2007 to 2017 compared to 1997 to 2007. In contrast, the genetic progress in Rubia Gallega, although positive, was smaller. The figure also highlights the genetic progress attributed to S+, which follows the same pattern as the global progress. This confirms that the main source of genetic advancement in both populations is the gene flow from S+, primarily comprising the sires selected for AI.

Another valuable feature of the Gibbs sampler output is the ability to calculate the posterior probability of a positive (or negative)

genetic response between two specific time points. Again this evidence the effectiveness of the selection applied in the whole population or a certain group. Additionally, a threshold genetic response can be settled and the probability of achievement can be calculated. This analysis can be also useful to replicate realistically selection by clusters in a breeding program simulation. To illustrate this, Figure 4 presents the posterior mean and the 95% HPDs for the yearly total genetic response for CONF in the Pirenaica population, as well as the genetic response attributed to S+ and DS clusters. Additionally, it displays (as a number) the posterior probability of a positive genetic response for each year.

The results in Figure 4 confirm the overall genetic trend for CONF in the Pirenaica population, with the posterior probability of a positive genetic trend exceeding 0.9 in most years. However, it is evident that the genetic trend was less pronounced between 1999 and 2003. Additionally, the posterior probabilities

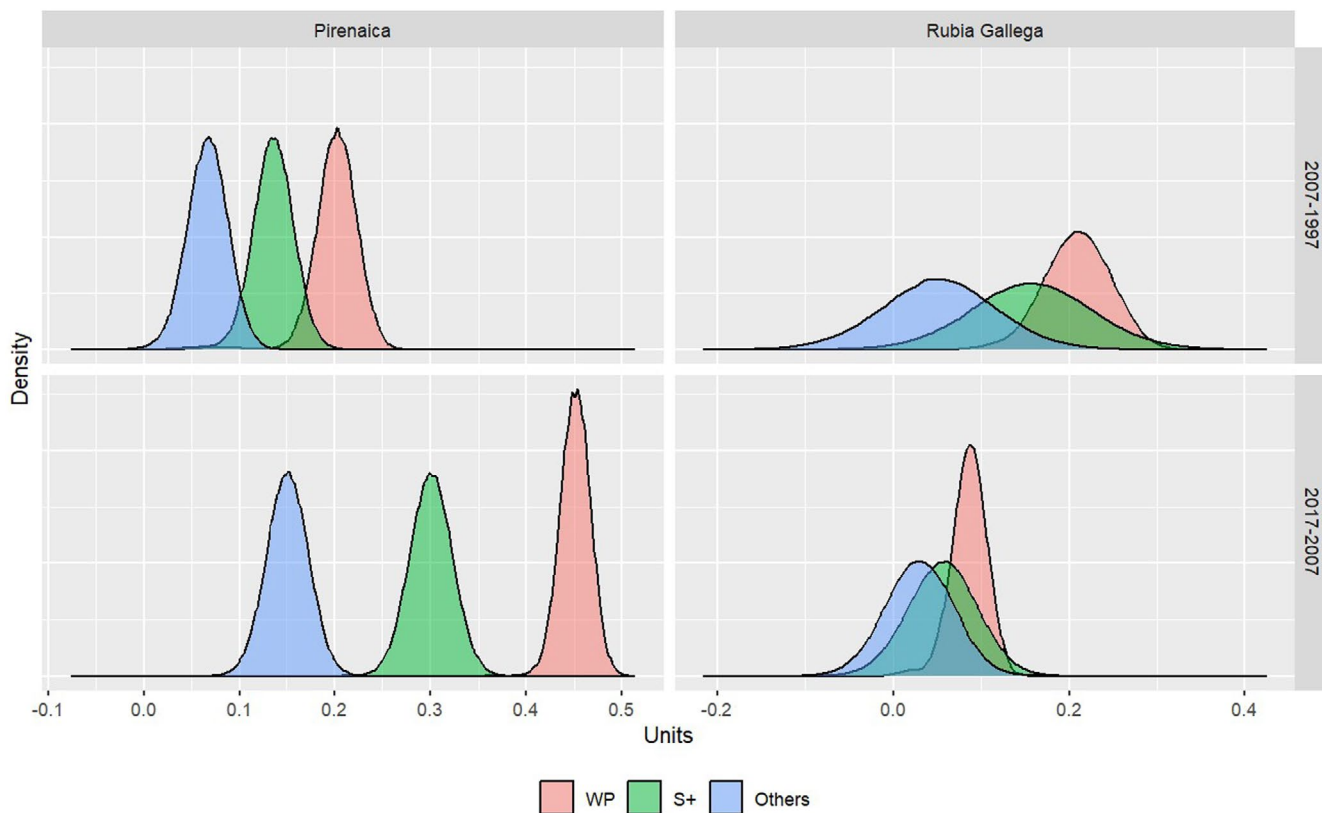


FIGURE 3 | Total genetic progress (WP, in red), associated with sires with progeny higher than 50 (S+, in green), and linked with the other clusters (Others, in blue) for Carcass Conformation and from 1997 to 2007 and from 2007 to 2017. [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

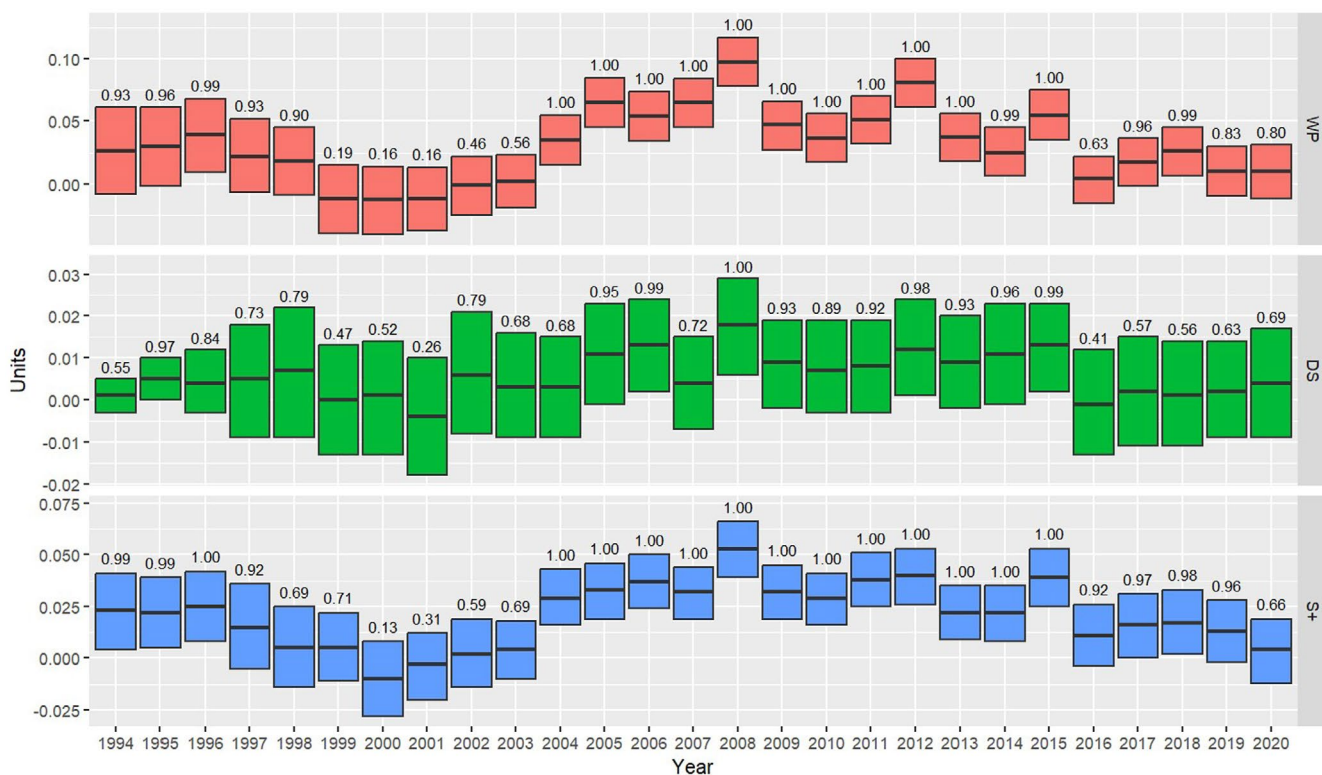


FIGURE 4 | Posterior mean, highest posterior densities (HPDs) at 95% and posterior probability over zero for the whole population (WP, in red), dams of sires (DS, in green), and sires with a progeny higher of 50 (S+, in blue) yearly genetic response for Carcass Conformation in the Pirenaica population. [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

of genetic response for the S+ and DS clusters corroborate these findings. For the S+ cluster, the posterior probability of a positive genetic response exceeded 0.9 in all years except from 1998 to 2003. Furthermore, the posterior probability of a positive genetic trend in the DS cluster was over 0.5 in almost all years, exceeding 0.9 in 10 of the 27 years analysed.

The posterior estimates of genetic trends rely on the cluster definition, which can be easily modified in the pedigree file. The simplicity of this definition facilitates the evaluation of breeding strategy efficiency across different clusters of individuals in animal and plant populations. Furthermore, multiple-trait analysis incorporates information from correlated traits and enables the study of genetic trends for all traits within a single analysis.

The TM_TRENDS software presented here calculates genetic trends using only genealogical information. Previous studies (Abdollahi-Arpanahi et al. 2021) estimating partitioned genetic trends have used breeding value solutions from a single-step GBLUP (Legarra et al. 2014), but, the numerator relationship matrix is applied to estimate partitioned genetic trends. The partitioning methodology (García-Cortés, Martínez-Ávila, and Toro 2008) is based on the recursive properties of the breeding value definition, allowing these values to be split into contributions from ancestors and Mendelian sampling terms. This recursive property does not hold with the genomic relationship matrix (\mathbf{G}), as defined by VanRaden (2008). However, Christensen et al. (2014) has adapted the concept of partial genetic matrix (García-Cortés and Toro 2006) to SNP marker-based partial genetic matrix. Therefore, the implementation of a procedure for partition the genetic trends into cluster should involve the definition a marker-based partial genetic matrix for each cluster of individuals in a similar way that is it performed in the genomic evaluation of crossbreeding populations (González-Diéguez et al. 2020; Mei et al. 2023).

4 | Conclusion

The TM_TRENDS software integrates the Bayesian calculation of partitioned genetic trends into the TM software (Legarra, Varona, and López de Maturana 2011), maintaining its flexibility in incorporating covariates, systematic and several environmental and genetic random effects in univariate or multivariate analyses, as well as for linear and threshold traits. Multiple founder groups can be also considered. The multiple trait model includes information across all correlated traits and reduces estimation bias by accounting for correlated selected traits. Moreover, the Bayesian implementation offers a more detailed inference of the global and partitioned genetic trend, as it accounts for the uncertainty in the variance components and provides all Gibbs samples of the global and partitioned genetic trends, which can be used for additional inferences. This tool opens new possibilities for exploring the dynamics of genetic trends and responses to selection in animal and plant populations.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available due to privacy or ethical restrictions.

References

- Abdollahi-Arpanahi, R., D. Lourenco, A. Legarra, and I. Misztal. 2021. "Dissecting Genetic Trends to Understand Breeding Practices in Livestock: A Maternal Pig Line Example." *Genetics, Selection, Evolution* 53: 89. <https://doi.org/10.1186/s12711-021-00683-6>.
- Altarriba, J., G. Yagüe, C. Moreno, and L. Varona. 2009. "Exploring the Possibilities of Genetic Improvement From Traceability Data. An Example in the Pirenaica Beef Cattle." *Livestock Science* 125: 115–120. <https://doi.org/10.1016/j.livsci.2009.03.013>.
- Antonios, S., A. Legarra, R. Pong-Wong, J. M. Astruc, S. T. Rodríguez-Ramilo, and Z. G. Vitezica. 2023. "Partitioning of the Genetic Trends of French Dairy Sheep in Mendelian Samplings and Long-Term Contributions." *Journal of Dairy Science* 106: 6275–6287. <https://doi.org/10.3168/jds.2022-23009>.
- Blair, H. T., and E. J. Pollak. 1984. "Estimation of Genetic Trend in a Selected Population With and Without the Use of a Control Population." *Journal of Animal Science* 58: 878–886. <https://doi.org/10.2527/jas1984.584878x>.
- Christensen, O. F., P. Madsen, B. Nielsen, and G. Su. 2014. "Genomic Evaluation of Both Purebred and Crossbred Performances." *Genetics, Selection, Evolution* 46: 23. <https://doi.org/10.1186/1297-9686-46-23>.
- García-Cortés, L. A., J. C. Martínez-Ávila, and M. A. Toro. 2008. "Partition of the Genetic Trend to Validate Multiple Selection Decisions." *Animal* 2: 821–824. <https://doi.org/10.1017/S175173110800205X>.
- García-Cortés, L. A., and M. Á. Toro. 2006. "Multibreed Analysis by Splitting the Breeding Values." *Genetics, Selection, Evolution* 38: 601–615. <https://doi.org/10.1051/gse:2006024>.
- González-Diéguez, D., L. Tusell, A. Bouquet, A. Legarra, and Z. G. Vitezica. 2020. "Purebred and Crossbred Genomic Evaluation and Mate Allocation Strategies to Exploit Dominance in Pig Crossbreeding Schemes." *G3: Genes, Genomes, Genetics* 10: 2829–2841. <https://doi.org/10.1534/g3.120.401376>.
- Henderson, C. R. 1984. "Applications of Linear Models in Animal Breeding." University of Guelph, Ontario, Canada.
- Hickey, J. M., M. G. Keane, D. A. Kenny, A. R. Cromie, and R. F. Veerkamp. 2007. "Genetic Parameters for EUROP Carcass Traits Within Different Groups of Cattle in Ireland." *Journal of Animal Science* 85: 314–321. <https://doi.org/10.2527/jas.2006-263>.
- Im, S., R. Fernando, and D. Gianola. 1989. "Likelihood Inferences in Animal Breeding Under Selection: A Missing-Data Theory View Point." *Genetics, Selection, Evolution* 21: 399. <https://doi.org/10.1186/1297-9686-21-4-399>.
- Inoue, K., M. Hosono, and Y. Tanimoto. 2017. "Inferring Causal Structures and Comparing the Causal Effects Among Calving Difficulty, Gestation Length and Calf Size in Japanese Black Cattle." *Animal* 11: 2120–2128. <https://doi.org/10.1017/S1751731117000957>.
- Legarra, A., O. F. Christensen, I. Aguilar, and I. Misztal. 2014. "Single Step, a General Approach for Genomic Selection." *Livestock Science* 166: 54–65. <https://doi.org/10.1016/j.livsci.2014.04.029>.
- Legarra, A., L. Varona, and E. López de Maturana. 2011. "Threshold Model."
- López-Carbonell, D., J. Altarriba, M. A. Ramírez, H. Srihi, and L. Varona. 2023. "Genetic Correlations Between Morphological and Reproductive, Growth and Carcass Quality Traits in the Pirenaica Beef Cattle Breed." *ITEA Informacion Tecnica Economica Agraria* 119: 225–243. <https://doi.org/10.12706/itea.2023.002>.

- Madsen, P., J. Jensen, R. Labouriau, O. F. Christensen, and G. Sahana. 2010. "DMU – A Package for Analyzing Multivariate Mixed Models in quantitative Genetics and Genomics." In *10th World Congress on Genetics Applied to Livestock Production*, 17–22. Vancouver, Canada.
- Martinez-Castillero, M., C. Then, J. Altarriba, et al. 2021. "Detection of Genomic Regions With Pleiotropic Effects for Growth and Carcass Quality Traits in the Rubia Gallega Cattle Breed." *Animals* 11: 1682. <https://doi.org/10.3390/ani11061682>.
- Mei, Q., H. Liu, S. Zhao, T. Xiang, and O. F. Christensen. 2023. "Genomic Evaluation for Two-Way Crossbred Performance in Cattle." *Genetics, Selection, Evolution* 55: 17. <https://doi.org/10.1186/s12711-023-00792-4>.
- Misztal, I., S. Tsuruta, D. Lourenco, I. Aguilar, A. Legarra, and Z. Vitezica. 2018. "Manual for BLUPF90 Family of Programs." University of Georgia, Athens, GA (USA).
- Obšteter, J., J. Holl, J. M. Hickey, and G. Gorjanc. 2021. "AlphaPart—R Implementation of the Method for Partitioning Genetic Trends." *Genetics, Selection, Evolution* 53: 30. <https://doi.org/10.1186/s12711-021-00600-x>.
- Obšteter, J., J. Jenko, I. Pocrnic, and G. Gorjanc. 2023. "Investigating the Benefits and Perils of Importing Genetic Material in Small Cattle Breeding Programs via Simulation." *Journal of Dairy Science* 106: 5593–5605. <https://doi.org/10.3168/jds.2022-23132>.
- Oliveira, T. P., J. Obšteter, I. Pocrnic, N. Heslot, and G. Gorjanc. 2023. "A Method for Partitioning Trends in Genetic Mean and Variance to Understand Breeding Practices." *Genetics, Selection, Evolution* 55: 36. <https://doi.org/10.1186/s12711-023-00804-3>.
- Piedrafito, J., R. Quintanilla, C. Sañudo, et al. 2003. "Carcass Quality of 10 Beef Cattle Breeds of the Southwest of Europe in Their Typical Production Systems." *Livestock Production Science* 82: 1–13. [https://doi.org/10.1016/S0301-6226\(03\)00006-X](https://doi.org/10.1016/S0301-6226(03)00006-X).
- R Core Team. 2021. "R: A Language and Environment for Statistical Computing." R Found. Stat. Comput. Vienna, Austria. <http://www.R-project.org/>.
- Škorput, D., G. Gorjanc, A. Kasap, and Z. Luković. 2015. "Partition of Genetic Trends by Origin in Landrace and Large-White Pigs." *Animal* 9: 1605–1609. <https://doi.org/10.1017/S1751731115001056>.
- Sorensen, D. A., and B. W. Kennedy. 1984. "Estimation of Response to Selection Using Least-Squares and Mixed Model Methodology." *Journal of Animal Science* 58: 1097–1106. <https://doi.org/10.2527/jas1984.5851097x>.
- Sorensen, D. A., C. S. Wang, J. Jensen, and D. Gianola. 1994. "Bayesian Analysis of Genetic Change due to Selection Using Gibbs Sampling." *Genetics, Selection, Evolution* 26: 333–360. <https://doi.org/10.1051/gse:19940403>.
- Srivastava, S., B. I. Lopez, S. D. L. Heras-Saldana, et al. 2019. "Estimation of Genetic Parameters by Single-Trait and Multi-Trait Models for Carcass Traits in Hanwoo Cattle." *Animals* 9: 1061. <https://doi.org/10.3390/ani9121061>.
- Thompson, R., and K. Meyer. 1986. "A Review of Theoretical Aspects in the Estimation of Breeding Values for Multi-Trait Selection." *Livestock Production Science* 15: 299–313. [https://doi.org/10.1016/0301-6226\(86\)90071-0](https://doi.org/10.1016/0301-6226(86)90071-0).
- Utrera, A. R., and L. D. Van Vleck. 2004. "Heritability Estimates for Carcass Traits of Cattle: A Review." *Genetics and Molecular Research* 3: 380–394.
- Van Tassell, C. P., and L. D. Van Vleck. 1996. "Multiple-Trait Gibbs Sampler for Animal Models: Flexible Programs for Bayesian and Likelihood-Based (Co)variance Component Inference." *Journal of Animal Science* 74: 2586–2597. <https://doi.org/10.2527/1996.74112586x>.
- VanRaden, P. M. 2008. "Efficient Methods to Compute Genomic Predictions." *Journal of Dairy Science* 91: 4414–4423. <https://doi.org/10.3168/JDS.2007-0980>.
- Woolliams, J. A., P. Bijma, and B. Villanueva. 1999. "Expected Genetic Contributions and Their Impact on Gene Flow and Genetic Gain." *Genetics* 153: 1009–1020. <https://doi.org/10.1093/genetics/153.2.1009>.

Supporting Information

Additional supporting information can be found online in the Supporting Information section.